or exponentially as

(ii) 
$$B_t = \frac{B_t \left( e^{G_t - Z_t - 1} \right)}{G_t - Z_t}$$

(Ricker 1975). The choice of calculation method may influence the yield estimates and consequently the determination of optimal levels of exploitation.

Ricker (1975) and Paulik and Bayliff (1967) alluded to the importance of the difference in magnitude between instantaneous growth and total mortality rates  $(G_t - Z_t)$ . They indicated that if the difference was small, arithmetic and exponential calculations approached one another. Ricker suggested using small intervals if the rates are rapidly changing. In this paper we 1) examine the difference in the two estimates of mean biomass as a function of the instantaneous rates of growth and mortality, and 2) reexamine the consequences of the choice of mean biomass estimates on estimates of equilibrium yield per recruit using data previously employed by Ricker (1975) and Paulik and Bayliff (1967), showing that under many conditions, exponential estimates of mean biomass are preferable.

The difference between arithmetic and exponential estimates of mean biomass increases rapidly as  $G_t - Z_t$  increases in a positive direction, but diverges less rapidly when  $G_t - Z_t$  increases in a negative direction. When  $B_t$  is arbitrarily taken in unity, the relationship is satisfactorily represented by a polynomial regression (Fig. 1).

With many fisheries it is only possible to estimate instantaneous fishing mortality  $(F_t)$  on an annual basis. Thus, a large interval must be used. The larger the interval, the more likely it is that  $G_t-Z_t$  is of a magnitude that would cause significant differences in estimates of  $\overline{B}_t$  calculated arithmetically and exponentially. Also, in heavily exploited fisheries there may be a large difference between growth and mortality rates within an interval especially at older ages.

We employed Ricker's (1975:242-243, table 10.3) example of bluegills from Muskellunge Lake to illustrate the difference between the two methods of computing mean biomass. This set was chosen because Ricker's data have been used previously as a historical data set and are readily available through his text. Mean biomass was computed arithmetically in the text example and also by Paulik and Bayliff (1967), who used the same data to introduce their computer program. We used the data in two separate runs to compute yield per

## ARITHMETIC VERSUS EXPONENTIAL CALCULATION OF MEAN BIOMASS

Mean biomass  $(\overline{B})$  within a time interval (t) is used in the Ricker method of estimating yield per recruit and can be calculated either arithmetically as

$$B_t = \frac{B_t + B_{t+1}}{2}$$

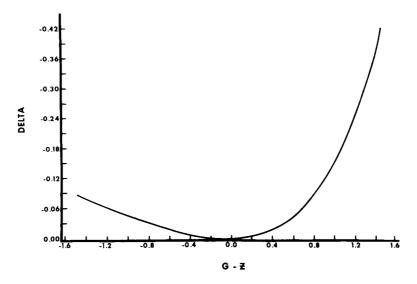


FIGURE 1.—Difference between arithmetic and exponential calculations of mean biomass when dt = 1.0 and  $B_t = 1.0$ , DELTA =  $B_t(B_t, \exp - B_{t, arith}) = B_t^* \{0.0061 + 0.0037 (G_t - Z_t) - 0.1095 ((G_t - Z_t)^2) - 0.0491 ((G_t - Z_t)^3)\}$ , r = 0.998.

recruit. In one,  $B_t$  was computed arithmetically, and in the other it was computed exponentially (Fig. 2). In both runs, the number of survivors was followed across the intervals and biomass was

tracked within each interval. There were obvious significant differences. Evaluating various F-multiples and ages of entry, when  $B_t$  was calculated arithmetically, the maximum yield exceeded the maximum biomass of the stock (5,522.6)

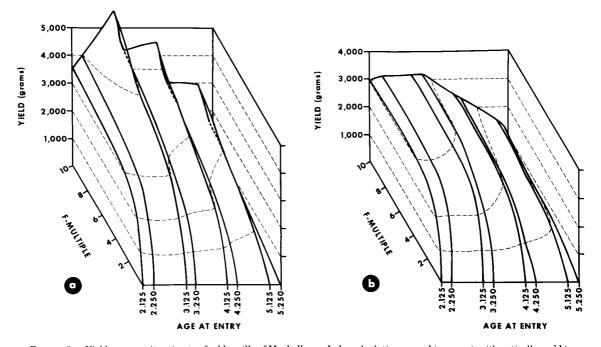


FIGURE 2.—Yield per recruit estimates for bluegills of Muskellunge Lake calculating mean biomass a) arithmetically and b) exponentially (data from Ricker 1975: table 10.3).

g vs. 3,439.2 g) when F-multipliers were large, which is impossible. Maximum biomass of the stock was estimated at F equals zero; the time intervals used were four one-eighth of a year intervals followed by one-half year intervals. Despite the small intervals, the difference between the yield per recruit estimates was large, indicating a need to minimize the  $G_t - Z_t$  difference if  $B_t$  is calculated arithmetically, regardless of the size of the time intervals. Therefore, in similar circumstances and for the example data set, we recommend that  $B_t$  be calculated exponentially.

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